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THE SURVIVAL OF *VAUCHERIA* (VAUCHERIACEAE) PROPAGULES IN DESICCATED NEW ENGLAND RIPARIAN SEDIMENTS

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ABSTRACT. Species of the algal genus *Vaucheria* routinely leave "seed banks" of propagules in riparian sediments for regrowth during optimal conditions in the habitat. Muds containing propagules were collected at different times of the year from four freshwater riparian habitats in central and eastern Connecticut, sites previously known to have as many as six *Vaucheria* species living sympatrically in the space of just 36 cm^2 of floodplain sediment or stream bank. Muds from each site were allowed to thoroughly desiccate in the laboratory. Desiccated mud samples were rehydrated after prescribed periods of time, and then cultured under optimal conditions in an incubator. Eight freshwater species appeared variously in the cultures demonstrating a tolerance to desiccation of 63–383 days with *V. undulata*, *V. prona*, and *V. frigida* surviving the greatest periods of treatment.

Key Words: desiccation tolerance, propagules, riparian sediments, seed banks, *Vaucheria*

Angiosperms—and in particular annuals—often accumulate seeds in soils as viable buried reserves or seed banks for when environmental conditions are optimal for germination (Begon et al. 1996). These seed banks allow flowering plants to survive periods of environmental stress, ensuring a species' eventual return to a normally suitable habitat. Such is the case when spring rains allow short-lived annuals to reappear in the desert. In wetlands, as water recedes from the margins of lakes, ponds, streams, and wet meadows, these habitats are often rapidly exploited by germinating seeds of grasses and herbaceous annuals that have broken dormancy (Keddy 2000). These are species requiring a greater soil O_2 content for germination than when inundated with water. When Darwin (1859) removed less than a full teacup of mud from the edge of an English pond, 537 seeds germinated in the next half year after allowing the mud to dry somewhat on his study windowsill. Such "seed banks" are also found among aquatic animals and protists that leave desiccation-resistant fertilized eggs or other propagules in habitats on a seasonal basis or when conditions are unsuitable for continued growth (Begon et al. 1996). In the New England terrestrial habitats where the yellow-green alga *Vaucheria* (Vaucheriaceae, Tribophyceae, Chrysophyta) grows, optimal wet conditions are not permanently sustained, and propagules that have been produced remain in the substrate as the "seed bank" for the next period of active growth after an interval of environmental stress such as desiccation.

Between 40–50 different species of *Vaucheria* have been reported from North America, with approximately three-quarters of these living in freshwater habitats and the remainder in brackish or marine waters (Blum 1972; Brown 1929). These algae are some of the most frequently encountered macroscopic terrestrial algae, dwelling on and in wet soils and muds throughout much of North America. In particular, *Vaucheria* species are common in riparian habitats, along stream and river banks and their associated floodplains. Under optimal conditions, dense, felt-like mats form, at times to 4–6 cm deep (Gallagher and Humm 1981), as populations grow throughout and above the substrate. *Vaucheria* mats frequently appear on the banks of streams and rivers, and it has been speculated that the coenocytic siphons aid in the prevention of bank erosion (Gallagher and Humm 1981; van den Hoek et al. 1995), as demonstrated for other terrestrial algae that bind soils together (Bailey et al. 1973; Cameron and Devaney 1970; Fletcher and Martin 1948). *Vaucheria* is also commonly found in disturbed habitats as a pioneer on newly exposed sediments such as floodplain marsh beds after deposition of new alluvium.

Unlike the periodic desiccation experienced by intertidal seaweeds, freshwater algae in riparian habitats experience periods of flooding and drought that are uncertain in length, making tolerance of water stress all the more crucial (Morison and Sheath 1985). Many studies have examined the germination of angiosperm seeds following periods of extended desiccation, but only a fraction have looked at the survival of freshwater algae in such circumstances. These investigations used air-dried agricultural soils that, when hydrated with nutrient media, ultimately produced cyanobacteria and green algae even after years of desiccation (Bristol 1919, 1920; Trainor 1970, 1985; Trainor and Gladych 1995). When examining the viability of terrestrial algae in some English soils, Bristol (1920) made the only report of *Vaucheria* surviving extended desiccation, finding *V. hamata* Vaucher after 45 days without moisture. Although not discussed or directly observed, one could assume the *Vaucheria* that appeared in Bristol's cultures was generated from a "seed bank" of propagules left by the alga during a period of abundant growth to survive periods of desiccation or other environmental stress.

A variety of structures produced by *Vaucheria* both sexually (oogamy) and asexually are encompassed by the term propagule, including the fertilized female oogonium (oospore), terminally "cut-off" vegetative fragments, aplanospores, and synzoospores (Greenwood 1959; Ott 1975; Rieth 1980). During periods of prolonged desiccation, it is possible that the cytoplasm concentrates within the coenocytic siphon and becomes separated by a wall, forming a dormant cyst-like structure commonly found in other groups of algae (Hoffmann 1989). Any of these propagules can be used to re-establish a population of *Vaucheria* when conditions for growth are suitable in the microenvironment. As *Vaucheria* is such a ubiquitous alga in riparian habitats, we have set out to test the ability of several species to tolerate water deprivation, a phenomenon that naturally occurs in the summer in New England floodplains.

STUDY AREAS

Four freshwater Connecticut sites were chosen based on previous collections of many sympatric *Vaucheria* species (Schneider et al. 1999):

1. Burlesson's Brook (BUR) — Suffield, Tolland Co., adjacent to Burlesson's Brook on Conn. Rt. 187 at the Connecticut-Massachusetts state line (42°02.063′N, 72°41.210′W);
2. Nipmuck Trail (NK) — Ashford, Windham Co., approximately 3 km from an entrance to the Nipmuck Trail, a portion of the Mohawk Trail system, on Conn. Rt. 74 (41°51.301′N, 72°12.821′W);
3. Scantic River (SCR) — Enfield, Tolland Co., floodplain directly beneath the bridge on Conn. Rt. 190 that crosses over

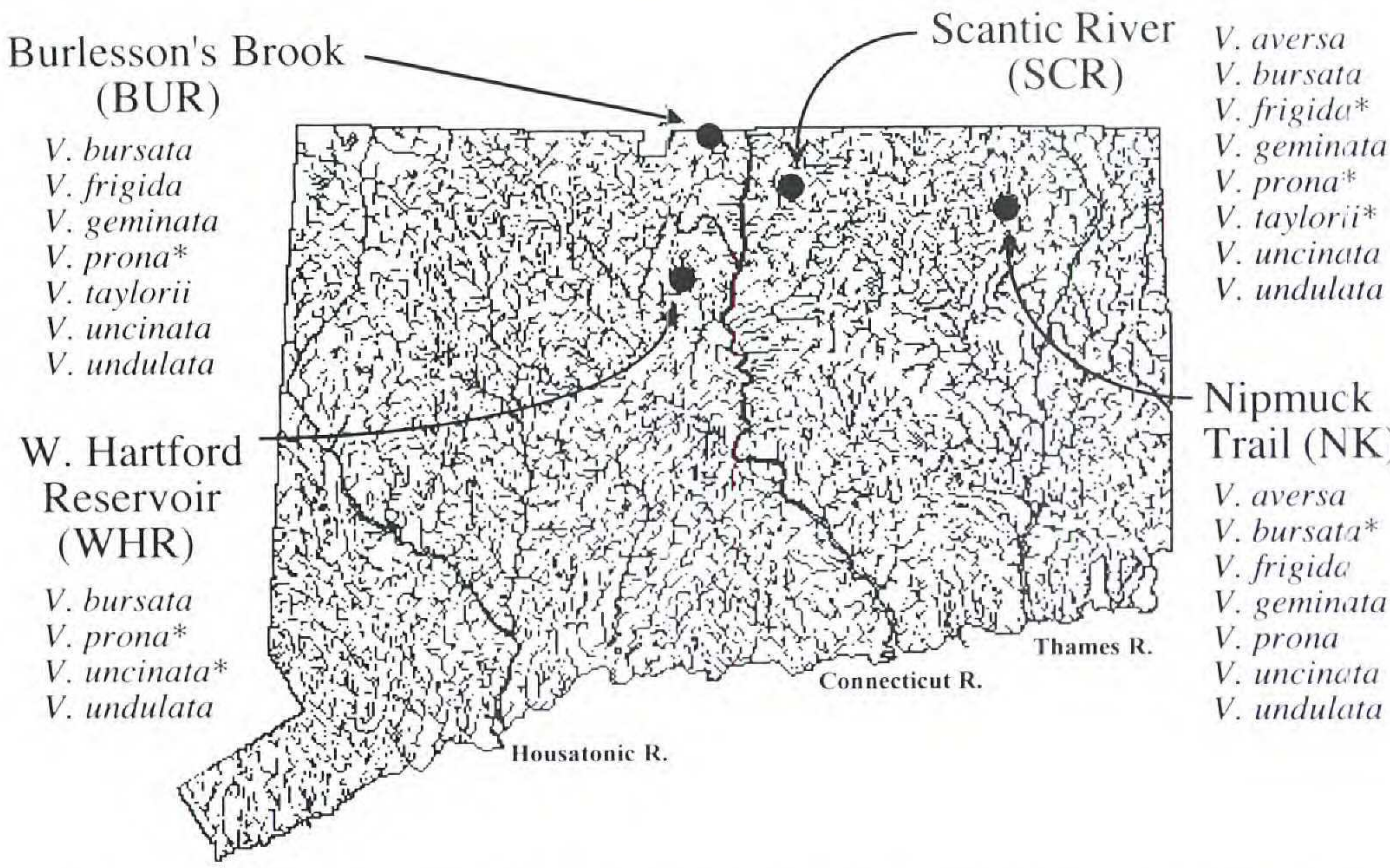

Figure 1. Connecticut, U.S.A. collection sites and their known *Vaucheria* species. Species discovered at each site for the first time are marked with an asterisk (*), the remainder are from Schneider et al. (1999).

the Scantic River near the intersection with Conn. Rt. 191 (41°58.966′N, 72°30.969′W);

4. West Hartford Reservoir (WHR) — West Hartford, Hartford Co., a low valley east of a recreational trail and the slow-moving stream outflowing from Wells Pond west of Conn. Rt. 44 and east of the reservoir (41°47.411′N, 72°47.099′W).

These sites are inhabited by eight of the eleven known freshwater species of *Vaucheria* found in Connecticut: *V. aversa* Hassall, *V. bursata* (O. F. Müll.) C. Agardh, *V. frigida* (Roth) C. Agardh, *V. geminata* (Vaucher) DC., *V. prona* T. A. Chr., *V. undulata* C. C. Jao, *V. uncinata* Kütz., and *V. taylorii* Blum (Figure 1). The remaining three freshwater species, *V. compacta* (Collins) Collins *ex* W. R. Taylor, *V. lii* Rieth, and *V. racemosa* (Vaucher) DC., have been observed only rarely in Connecticut and were not included in this study (Schneider and Lane 2000; Schneider et al. 1999).

MATERIALS AND METHODS

Longitude and latitude were fixed using a Garmin™ GPS 12 (vers. 4.57). At each of the four sites, bulk samples of the top 3–

4 cm of damp/wet mud from several locations were collected, with or without visible *Vaucheria* siphons, using a flat-nosed shovel. Mud was taken during all seasons except winter when substrates were frozen (ix.98, iii.99, vi.99). In the lab, 20–30 ml of water were added to the bulk samples so they could be thoroughly mixed. The mud slurry was then spread evenly to a depth of 1.5–3.0 cm in a 42.5 × 35.0 cm photographic developing tray, and left exposed to desiccate at 23–25°C. After the mud had dried for 3–4 days, it was cut into squares approximately 36 cm^2. The blocks were then left to dry in the trays until ready for rehydration. Every 5–20 days after partitioning into blocks, desiccated mud samples from each site and collection date were placed in plastic culture dishes (3.5 × 8.5 cm) and rehydrated with Bold's basal medium (Bischoff and Bold 1963), such that approximately 0.5–1.0 cm standing medium remained in the dish after mud saturation. For the purposes of this study, "days desiccated" (Table 1) refers to the amount of time from partitioning of the blocks in the exposed trays to rehydration, although the mud was not completely desiccated for the first week. In order to establish which *Vaucheria* species were present in the mud samples to be desiccated, control cultures of the same size were established from each site and sampling date. The controls were immediately placed into individual culture dishes with Bold's medium.

All culture dishes were incubated in a Hotpack™ growth chamber under a 16L:8D diurnal cycle at 15°C, with cool white fluorescent lights and an irradiance level of 3.49–16.58 $\mu mol/m^2/sec$, conditions found optimal for the growth of a wide variety of *Vaucheria* species (Schneider et al. 1993, 1999). Cultures were examined for *Vaucheria* siphons using a dissecting microscope every 7–10 days. As siphons appeared, small amounts were removed for examination under a compound microscope to search for gametangia—characteristics used to distinguish species.

RESULTS

Most of the experimental cultures became reproductive, allowing the identification of 4–7 species at every site. *Vaucheria* collected in muds from all four sites was shown to tolerate desiccation for a period of nearly 200 days, with propagules of *V. undulata* from SCR showing the greatest tolerance, surviving 383 days of desiccation (Table 1), followed by *V. prona* (359 days)

Table 1. Desiccation tolerance (in days) of eight *Vaucheria* species in mud collected on several dates from four Connecticut riparian sites. Collection site abbreviations are defined in the text and Figure 1. Brackets indicate that the species appeared in control cultures for the collection at that site. Data for species appearing in experimental dishes that did not appear in the accompanying control dishes are listed without brackets.

Species	No. of Days of Desiccation Tolerated								
Coll. Site:	BUR I	BUR II	BUR III	NK I	NK II	SCR I	SCR II	WHR I	WHR II
Coll. Date:	iii.99	vi.99	x.99	ix.98	vii.99	vi.99	x.99	vi.99	x.99
Vaucheria aversa	–	–	–	[41]	145	[110]	94	–	–
Vaucheria bursata	[–]	[130]	84	–	[91]	119	94	59	–
Vaucheria frigida	[–]	[49]	189	[12]	[49]	320	–	–	–
Vaucheria geminata	–	–	56	–	–	16	144	–	–
Vaucheria prona	–	49	219	22	[59]	[359]	154	[133]	–
Vaucheria taylorii	–	[–]	–	–	–	–	63	–	–
Vaucheria uncinata	–	[118]	30	[18]	[–]	16	–	193	–
Vaucheria undulata	[178]	[198]	219	[229]	[99]	[383]	154	[193]	68
Vaucheria spp.	240	198	219	229	153	383	154	193	72

and *V. frigida* (320 days). *Vaucheria* survived desiccation for 240 days at BUR, 229 days at NK, and 193 days at WHR. Among the species, *V. undulata* again survived the longest treatment in all but one collection at these three sites (Table 1). In the NK II mud sample, *V. aversa* showed the greatest tolerance to desiccation (145 days).

Certain species previously known from a site (Schneider et al. 1999) never appeared in either the control or experimental dishes of the present study: *Vaucheria geminata* at NK and WHR, *V. aversa* at BUR and WHR, and *V. taylorii* from SCR. Presumably, these species had not left a significant "seed bank" in the sediments prior to each of the collections to allow a new population to flourish, as even the controls did not produce them. Conversely, some species were discovered in our cultures that had not previously been found at each site, including *V. prona* from BUR, SCR, and WHR. These species are marked with asterisks (*) in Figure 1. In the present study, 50–80 mud blocks from each site were rehydrated over time, increasing the likelihood that a species might appear due to the greater sample size. The most infrequently discovered species, *V. taylorii*, previously known only at BUR among the four sites, appeared in a BUR II control dish and in SCR II after 63 days of desiccation. Several other species appeared in the desiccated mud blocks of each site and not the control cultures of the same collection (Table 1, number of days not bracketed), or in the controls but not the rehydrates (Table 1, bracketed dashes).

DISCUSSION

The genus *Vaucheria* is widely distributed throughout North America except in areas with prolonged drought such as the southwestern United States. Prescott (1938) suggested that terrestrial species of *Vaucheria* favor habitats where adequate precipitation, humidity, and cold temperatures are found, but the alga can also thrive where average surface temperatures reach as high as 50°C, providing sufficient water content is present in the substrate. Unlike algae with partitioned filaments, *Vaucheria* has the ability to allow unrestricted cytoplasmic flow within a coenocytic siphon, allowing the transport of water, CO_2, and nutrients to portions of the alga which are above the surface of the substrate, and O_2 and photosynthetic products to portions below the mud.

Therefore, although parts of an alga might not have access to optimum conditions for photosynthesis or nutrient/water uptake, *Vaucheria* may still be able to grow optimally due to its exposure to both the substrate and atmospheric environments.

Previous studies of *Vaucheria* have demonstrated a staggered emergence of different species, attributed to competitive interactions with biological and seasonal changes (humidity, temperature, water content in soil) further regulating the development (Nienhuis and Simons 1971; Schneider et al. 1999; Simons 1975). It is possible that higher numbers of propagules are produced and released in the winter and spring when moisture and nutrient contents in the soil are high (Islam 1984). In fact, many species of *Vaucheria* are reported by Blum (1972) to be reproductive only in winter through spring in North America. Nevertheless, in the present study, the time of mud collection seemed to have little effect on the species ultimately appearing in our cultures (Table 1), perhaps due to the abundance of ungerminated propagules in our mud sample "seed banks" whenever collected. Not all of the species in this study produced robust "seed banks"; thus, their survival during desiccation can hardly be considered definitive. *Vaucheria taylorii* appeared in only two of the 261 total dishes from all of the sites, presumably showing its lesser presence in the *Vaucheria* "seed bank." Whether 63 days of survival is near the high end of success this species can attain is difficult to know based upon its presumed small number of propagules in the collected muds.

We have been able to demonstrate that eight Connecticut species of *Vaucheria* were able to survive extended periods of desiccation in a controlled laboratory experiment. *Vaucheria undulata* tolerated desiccation for 383 days and *V. prona* for 359 days, periods eight times longer than that demonstrated by Bristol (1920) for *V. hamata*. The results we present for each of the species show the survival of *Vaucheria* propagules to a specific environmental stress far beyond what would normally impinge upon species in a temperate, seasonally variable, generally moist New England environment, where such prolonged periods of drought are unlikely to occur under normal circumstances. Given the results presented here, desiccation does not appear to be a limiting factor to the success of *Vaucheria* in a given habitat, providing it has initially established a reproductive population and buried a "seed bank" of propagules.

It is interesting to note that the two *Vaucheria* species that appeared most frequently in our desiccated mud samples, *V. prona* and *V. undulata*, are in fact the most widely distributed and commonly collected species in Connecticut (Schneider et al. 1999). *Vaucheria undulata* was the only species to appear in each of the nine desiccated mud samples (Table 1). In our rehydrated cultures, *V. prona* and *V. undulata* were observed to occur simultaneously with great frequency at each of the four collection sites, and until their reproductive periods had concluded, often with virtually complete exclusion of all other *Vaucheria* species. *Vaucheria uncinata* and *V. bursata* were also found at all four sites (Figure 1). The appearance at different times, and establishment of these species in the mud cultures for varying lengths of time, may indicate that certain species can outcompete others for available nutrients, water, or substrate. However, there is no way to guarantee that propagules of all of the species were evenly spread throughout the original bulk samples from each site, a concern inherent with our experimental procedures. Furthermore, a single mud sample taken at one point during the year may be unable to accurately reflect diversity and abundance of the total algae present at a given site (Hunt et al. 1979), as the "seed bank" is replenished by the varied species actively growing at different times of the year. For example, the desiccated muds from WHR collected in June produced four species of *Vaucheria*, while October samples from the same site produced only one (Table 1). Reproductive periodicity caused by intraspecific or other mechanisms can cause what Hoffmann (1987) described as a temporal and spatial patchiness of "propagule rain." The abundance of a particular species' propagules is therefore dependent upon its seasonal or periodic reproduction. Persistent seed pools in the soil are characteristic of ephemeral flowering plants in unpredictable habitats (Barbour et al. 1999), and *Vaucheria* seems to conform to this ecological strategy. The successful development of eight species in our severely desiccated mud samples from all four sites over extended time demonstrates a remarkable ability for survival by *Vaucheria* propagules to overcome an important environmental stress and be able to grow and succeed when conditions improve.

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LITERATURE CITED

Bailey, D., A. P. Mazurak, and J. R. Rosowski. 1973. Aggregation of soil particles by algae. J. Phycol. 9: 99–101.

Barbour, M. G., J. H. Burk, W. D. Pitts, F. S. Gilliam, and M. W. Schwartz. 1999. Terrestrial Plant Ecology, 3rd ed. Addison Wesley Longman, Inc., Menlo Park, CA.

Begon, M., J. L. Harper, and C. R. Townsend. 1996. Ecology, 3rd ed. Blackwell Science, Ltd., Oxford, UK.

Bischoff, H. W. and H. C. Bold. 1963. Phycological studies IV. Some soil algae from Enchanted Rock and related algal species. Univ. Texas Publ., No. 6318, Austin, TX.

Blum, J. L. 1972. North American Flora, Series 2, Part 8: Vaucheriaceae. The New York Botanical Garden, Bronx, NY.

Bristol, B. M. 1919. On the retention of vitality by algae from old stored soils. New Phytol. 18: 92–107.

———. 1920. On the algae-flora of some desiccated English soils: An important factor in soil biology. Ann. Bot. (London) 34: 35–80.

Brown, H. J. 1929. The algal family Vaucheriaceae. Trans. Amer. Microscop. Soc. 48: 86–117.

Cameron, R. E. and J. R. Devaney. 1970. Antarctic soil algal crusts: Scanning electron and optical microscope study. Trans. Amer. Microscop. Soc. 89: 264–273.

Darwin, C. 1859 [reprinted 1979]. On the Origin of Species by Natural Selection, or the Preservation of Favoured Races in the Struggle for Life, 1st ed. Avenel Books, New York.

Fletcher, J. E. and W. P. Martin. 1948. Some effects of algae and molds on the rain crust of desert soils. Ecology 29: 95–100.

Gallagher, S. B. and H. J. Humm. 1981. *Vaucheria* (Xanthophyceae, Vaucheriaceae) of the Central Florida Gulf Coast. Bull. Mar. Sci. 31: 184–190.

Greenwood, A. D. 1959. Observations on the structure of the zoospores of *Vaucheria* II. J. Exp. Bot. 10: 55–68.

Hoffmann, A. J. 1987. The arrival of seaweed propagules at the shore: A review. Bot. Mar. 30: 151–165.

Hoffmann, L. 1989. Algae of terrestrial habitats. Bot. Rev. (Lancaster) 55: 77–105.

Hunt, M. E., G. L. Floyd, and B. B. Stout. 1979. Soil algae in field and forest environments. Ecology 60: 362–375.

Islam, A. K. M. 1984. Studies on the genus *Vaucheria*. Int. Rev. Gesamten Hydrobiol. 69: 877–902.

Keddy, P. A. 2000. Wetland Ecology: Principles and Conservation. Cambridge Studies in Ecology. Cambridge Univ. Press, Cambridge, UK.

Morison, M. O. and R. G. Sheath. 1985. Responses to desiccation stress by *Klebsormidium rivulare* from a Rhode Island stream. Phycologia 24: 129–145.

NIENHUIS, P. H. AND J. SIMONS. 1971. *Vaucheria* species and some other algae on a Dutch salt marsh, with ecological notes on their periodicity. Acta Bot. Neerl. 20: 107–118.

OTT, D. W. 1975. Developmental cytology of the genus *Vaucheria* III. Emergence, settlement and germination of the mature zoospore of *V. fontinalis* (L.) Christensen. Brit. Phycol. J. 10: 49–56.

PRESCOTT, G. W. 1938. A new species and a new variety of the algal genus *Vaucheria* DC. with notes on the genus. Trans. Amer. Microscop. Soc. 57: 1–11.

RIETH, A. 1980. Xanthophyceae. Part 2. *In:* H. Ettl, J. Gerloff, and H. Heynig, eds., Süβwasserflora von Mitteleuropa, Vol. 4. Gustav Fischer Verlag, Stuttgart, Germany.

SCHNEIDER, C. W. AND C. E. LANE. 2000. Two species of *Vaucheria* new for New England, *V. lii* and *V. racemosa*. NorthE. Naturalist 7: 25–32.

———, ———, AND A. NORLAND. 1999. The freshwater species of *Vaucheria* (Tribophyceae, Chrysophyta) from Connecticut. Rhodora 101: 234–263.

———, L. A. MACDONALD, J. F. CAHILL, JR., AND S. W. HEMINWAY. 1993. The marine and brackish water species of *Vaucheria* (Tribophyceae, Chrysophyta) from Connecticut. Rhodora 95: 97–112.

SIMONS, J. 1975. Periodicity and distribution of brackish *Vaucheria* species from non-tidal coastal areas in the S.W. Netherlands. Acta Bot. Neerl. 24: 89–110.

TRAINOR, F. R. 1970. Survival of algae in a desiccated soil. Phycologia 9: 111–113.

———. 1985. Survival of algae in a desiccated soil: A 25 year study. Phycologia 24: 79–82.

——— AND R. GLADYCH. 1995. Survival of algae in a desiccated soil: A 35 year study. Phycologia 34: 191–192.

VAN DEN HOEK, C., D. G. MANN, AND H. M. JAHNS. 1995. Algae: An Introduction to Phycology. Cambridge Univ. Press, Cambridge, UK.